the forest is detected faster because it is larger than its component trees.

Several factors may have contributed to the faster IT selectivity for larger shapes. To match the locations of the single shapes to those of the local and global shapes in the hierarchical stimuli, the small and large shapes were centered at different retinal positions. The possibility cannot be excluded that responses to a peripherally-centered shape shows a longer latency than a centrally-positioned shape. Apart from their differences in size, large and small shapes also differ in spatial frequency content, and resolving features of a small shape requires higher spatial frequencies than does a large shape. Response latencies of primary visual cortical neurons (area V1) are shorter for low than for high spatial frequencies [17], which fits the shorter latency observed for the large-shape selectivity in the IT study. Overall, the earlier emergence of selectivity for large shapes agrees with the proposal [18] that the visual world is first analyzed at a coarse scale before turning to its finer details: first the rough outline of the forest, and then the trees, followed by twigs and leaves.

Macaque monkeys show a global-advantage effect in their behavioral reaction times [19]. Is the earlier-appearing selectivity for larger shapes observed in macaque IT related to the behavioral global-advantage effect? Because the study by Sripati and Olson [10] was performed in animals that were passively fixating during the recordings but were not performing a shape discrimination task, we do not know whether the responses of the IT neurons relate to the perceptual global advantage. This missing link needs to be addressed in future studies.

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Behavioural Ecology: Noise Annoys at Community Level

A new study on the impact of anthropogenic noise on birds takes a behavioural discipline to the level of community ecology: noise can not only harm individual species but also alter species relationships.

Hans Slabbekoorn and Wouter Halfwerk

Anthropogenic noise can be detrimental to many animal species in urbanized areas through stress, disturbance, or masking, but this impact is hard to study independently. As they report in this issue of *Current Biology*, Francis *et al.* [1] have tackled this issue in a new study of avian communities at noisy and relatively silent natural gas extraction sites, avoiding the typical confounding factors associated with highways or cities. The study not only confirmed that anthropogenic noise can have negative effects on breeding density for several species, but also demonstrated positive effects on other species that seem to benefit from a noise-associated decline in their major nest-predator. This impact of noise goes beyond the perils for single species and indicates anthropogenic infiltration at community level.

Elevated noise level through anthropogenic activity is a global phenomenon and probably only hearing-impaired people can say they have never experienced it. It is so common that most of us are habituated to unnaturally high noise levels. Many city-dwellers are even able to enjoy some sort of 'perceptual quietness' despite high decibel levels, for example when traffic noise is mixed with the wide-band noise of a city fountain and traffic is visually shielded by vegetation. But when the transmission of an important message depends on acoustics, the appreciation of noisy soundscapes changes dramatically. Just imagine

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Figure 1. Two examples of the study system in the pinyon-juniper woodlands of northwest New Mexico.

The picture on the left shows a silent control site with the constructions associated with gas extraction and transportation at a natural gas well. The picture on the right illustrates a very similar treatment site, with an additional noise-producing compressor (indicated by the white arrow). (Photos courtesy of Clinton Francis.)

a situation in which masking noise renders your call powerless to reach a child that is about to cross a street, ignorant of cars approaching at high speed.

Singing birds depend continuously on acoustics for communicating a message that can be critical to survival in a territory providing food, shelter, and nesting opportunities. Also, mate attraction is typically guided by acoustic signals: female birds often find a male of the right species and of the preferred quality by ear. Other important acoustic interactions concern begging by nestlings or fledglings, food and alarm calling, and production of contact calls that can be critical to group cohesion. Being able to hear rustling prey or hunting predators will also heavily affect chances of survival and reproduction, adding to the potential impact of masking noise on individual success and population viability [2].

The effect of anthropogenic noise on birds is typically studied in a context of dramatic habitat conversion associated with building roads and cities. Indeed, highways show a negative impact on bird breeding density and diversity, which may be attributed to the road-associated rise in noise level [3]. Urbanisation leads to the same set of common bird species present in cities everywhere, largely independent of the locality-specific original avifauna [4,5]. This homogenization may also be partly due to urban noise excluding sensitive species and providing opportunity to behaviourally flexible species [6,7]. However, there are many factors that are potentially playing a role in species decline and community change, most notably landscape turnover, but also chemical pollution, visual disturbance by people or car traffic, and introduction of human-associated food (for example, bread and peanuts) or predators (such as cats and dogs). Studies excluding all such confounding factors are required to confirm that anthropogenic noise itself is really harmful to birds.

Natural areas exploited for soil resources by the gas industry provide an interesting and unique model system to study the impact of noise pollution on birds. Typically, gas extraction stations are numerous and scattered throughout a large geographic area. Interestingly, only a subset of these stations are equipped with compressors that generate a loud low-frequency noise 24/7 (Figure 1). The decision to place a compressor at a certain site is based on gas well pressure and is made irrespective of above-ground variation in vegetation and other micro-climatic characteristics. Therefore, any difference between noisy compressor stations and relatively silent well pads, in bird density, diversity, or breeding success, can be attributed solely to the impact of noise.

A few years ago, the first study of this kind was conducted in a boreal mixed woodland forest in northeastern Alberta, Canada. In a single-species study, male ovenbirds (*Seiurus aurocapilla*) were shown to have a 17% reduction in mate attraction probability at noisy compressor sites compared to noiseless well pads [8]. Furthermore, they also monitored the avian communities near (100–300 m) and far (400–700 m) from gas extraction stations. Several species revealed the lowest densities in the 'near-noisy' condition, and this condition also turned out to have significantly lower overall breeding densities than 'far-noisy', 'near-quiet', and 'far-quiet' conditions [9].

In their new paper, Francis *et al.* [1] report on another location of gas extraction stations in pinyon-juniper woodlands of northwestern New Mexico, USA. In contrast to the earlier study, the analysis was not broken down to monitoring groups that were near and far away from stations, nor was there an overall decline in breeding density for the avian community near noisy compressor sites. Nevertheless, several species were shown to nest at larger distances from the station at noisy sites (monitored within a 400 m radius) compared to noiseless control sites. Interestingly, in this study a significant reduction in species

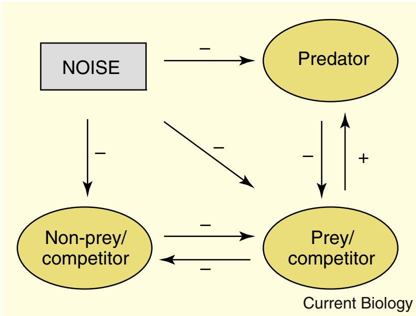

Figure 2. A species interaction web for three model bird species, including a predator–prey and a two-competitor relationship.

Arrows indicate either negative (–) or positive impact (+) on each other between species, and a negative impact of noise on all three species.

diversity at noisy compressor sites indicated a dramatic change in the avian community which was not reported for the Canadian location.

Insight into changes at community level driven by the presence of anthropogenic noise is the major step forward here (Figure 2). While several species show an expected decline in breeding density at noisy sites compared to noiseless sites, there are also species that show the opposite pattern. The authors argue that this noise-associated incline for several small songbird species may be explained by an indirect positive response through predator-release. The main reason for nest failure across species was nest predation by the Western scrub-jay (*Apheocoma californica*). The jay is also one of the species not doing well in noisy conditions and the probability of depredation turned out to be significantly lower in the noisy sites with less jays. This indirect positive effect may explain why these species do relatively well at compressor sites, not excluding the possibility of a direct negative impact of noise.

Besides the typical predator–prey relationship, in which high predator numbers negatively affect the prey population and high prey numbers positively affect the predator population (for example [10,11]), there could be more relationships pushed out of balance by noise. Although it may not be very obvious in the current model system, two or more species may compete for the same resources, such as nest sites, food sources, or hiding places (for example, [12,13]) or may share the same predator in so-called apparent competition [14]. Two such competitor species can negatively affect each other through competitive exclusion (Figure 2). Consequently, detrimental effects of anthropogenic noise that hit one species harder than the other may lead to improved conditions for the other through competitive release. Again, this may explain a noise-associated incline in one species (or the lack of a decline) despite a direct negative impact on both competitor species.

Direct and indirect effects in species relationships and the associated complexity are a well-known problem in community ecology, for example with multi-level trophic cascades or multi-species competitive interactions [15–17]. There are some community-level studies addressing human impact on birds, for example showing a shift from specialist to generalist species adjacent to walking trails [18]. However, the unique sampling opportunities unintentionally provided by the gas industry yield an interesting tool to study avian community ecology in a way similar to classic fertilizer experiments in plants (for example, [19,20]).

The integration of the behavioural study of noise impact on animal communication with community ecology reveals clearly how much anthropogenic noise can affect the ecological integrity of whole ecosystems. The new insights not only confirm that noise can be harmful, independent of confounding factors, but also tell us that we should not be surprised to find inconsistent results for single species when studied in different communities. From now on, we should realize that noise impact studies can involve complex relationships and that a thorough insight into local community ecology is required. This certainly means that translating data to conservation implications will be more challenging, but makes it all the more important.

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